THE VEGETATION OF THE SERRANÍA DE MACUIRA, GUAJIRA, COLOMBIA: A CONTRAST OF ARID LOWLANDS AND AN ISOLATED CLOUD FOREST
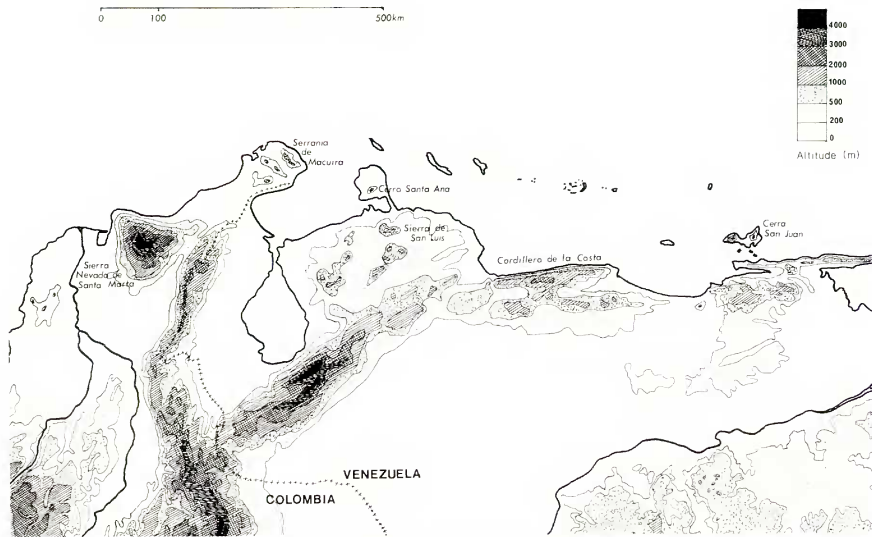
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In the Northeast Trade-Wind Belt on the Caribbean coast of South America, there are a number of small, isolated mountains and ranges of hills that are encompassed by arid lowlands and yet support humid vegetation on their upper slopes and summits. Notable among these are Cerro San Juan,[1] on Isla Margarita, Edo. Nueva Esparta, Venezuela (Johnston, 1909); Cerro Santa Ana, on the Península de Paraguaná, Edo. Falcón, Venezuela (Tamayo, 1941); and the Serranía de Macuira, at the northeastern extremity of the peninsula of Guajira, Colombia (Map 1). These mountains are geologically distinct from the Andes and the Venezuelan Cordillera de la Costa and are less than 1000 m high.

The summit vegetation of these hills is characterized by its low canopy, generally not exceeding 10 m; its gnarled, stunted trees with coriaceous leaves; and an abundance of vascular epiphytes. Rainfall is more or less restricted to a two-month season, and the vegetation depends upon daily orographic cloud cover resulting from the condensation of water vapor as the air is forced rapidly upward over the mountains by the strong winds. Precipitation is due to interception of wind-borne suspended water droplets by the vegetation and continues throughout the nine- or ten-month dry season prevailing in the surrounding lowlands, where the annual rainfall is less than 1000 mm.

The dependence of these forests on cloud interception (rather than rainfall) and their low altitude combine to produce a very remarkable circumstance. Cloud forests, which can be broadly defined as any montane forests frequently enshrouded by clouds and fog, are generally associated with higher elevations (> 1500 m), particularly in the Andes, and consequently with

[1]Presently called Cerro Copey.

MAP 1. Caribbean Colombia and Venezuela.

Labels on map:
Serranía de Macuira
Cerro Santa Ana
Sierra de San Luis
Cordillera de la Costa
Cerro San Juan
Sierra Nevada de Santa Marta
VENEZUELA
COLOMBIA

0   100   500km

4000
3000
2000
1000
500
200
0
Altitude (m)

lower temperatures. Where they do occur at lower altitudes (< 1500 m)—for instance, on the mountains east of the Canal Zone in Panama (Myers, 1969), the Northern Range in Trinidad (Beard, 1946), and the Luquillo Mountains, Puerto Rico (Howard, 1968)—they are surrounded by moist or semimoist lower montane and lowland rain forests rather than by very dry zones. In most places cloud interception is not a primary source of water (Kerfoot, 1968; Rutter, 1975); rather, it has the secondary although important effect of maintaining high humidity during periods of negligible rainfall, thus ensuring the survival of the abundant epiphytes that are almost diagnostic of cloud forest (Walter, 1973; Grubb, 1977; Sugden & Robins, 1979). By contrast, on the low coastal mountains on the Caribbean coasts of Colombia and Venezuela, cloud cover sustains "islands" of moist evergreen forest in the midst of highly seasonal vegetation zones. This paper concerns the summit vegetation of the Serranía de Macuira, the most western of these "islands."

GEOGRAPHY AND GEOLOGY

The peninsula of Guajira is the northernmost extension of the South American continent (Map 2). It is bounded by the Caribbean Sea to the north and east, the Gulf of Venezuela to the southeast and south, the Montes de Oca and the Sierra de Perijá to the southwest, and the Sierra Nevada de Santa Marta to the west. Except for a strip of the southeastern coast, which is Venezuelan territory, the peninsula lies within the borders of Colombia. It is as yet a largely undeveloped region because of its aridity and the scarcity of fresh water. Indians of the Guajiro tribe are the almost exclusive inhabitants of the peninsula. Previously nomadic pastoralists, they are now more sedentary as a result of improved communications, profitable commercial enterprises, and more reliable water supplies due to the advent of windpumps.
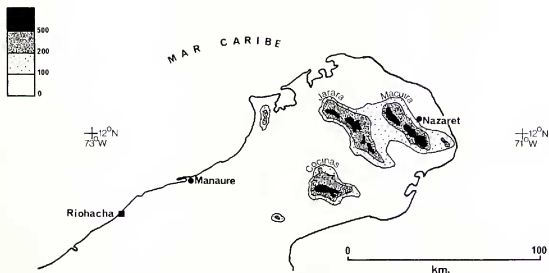
Map 2. The Guajira Peninsula, Colombia (contours in meters).

Guajira is predominantly flat, rising only a few meters above sea level, and is covered by Quaternary sand deposits. The flat plains are interrupted in the Alta Guajira (the bulging northeastern end of the peninsula) by three ranges of hills: the Serranía de Cocinas, the Serranía de Jarara, and the Serranía de Macuira (MAP 2). The Serranía de Macuira is the highest of the
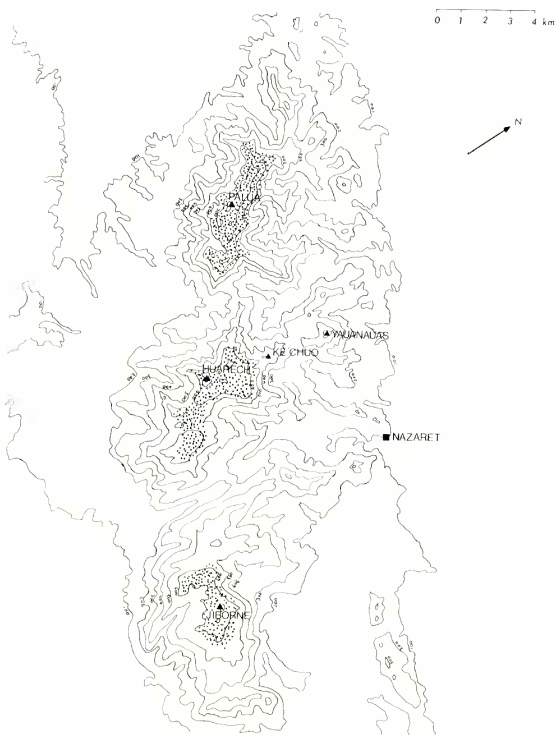
MAP 3. The Serranía de Macuira. Stippled areas represent approximate extent of Cloud Forest (contours in meters).

three, attaining a maximum elevation of 865 m. It was uplifted during the Late Cretaceous and consists mainly of metamorphic micaceous schists and granodiorites (Macdonald, 1964). Cretaceous limestones cap some of the outlying hills on the northeastern flanks of the range. The Serranía de Macuira is about 30 km long and 10 km across at its widest point, with the long axis lying northeast to southwest (Map 3).

The slopes of the Serranía de Macuira are characteristically very steep. The highest peaks, Jiborne (735 m), Huarech (853 m), and Palua (865 m), are separated from each other by several kilometers of deeply dissected terrain (Map 3). In the immediate vicinity of these peaks, the ground is more finely divided into a labyrinth of miniature valleys that run in a bewildering variety of directions and eventually flow together to descend into the deep valleys leading to the surrounding plains. The wide watercourses that flow from the Serranía are dry for most of the year, becoming impassable torrents several meters deep during and immediately after the brief rains. On the northeastern flank the slopes are largely covered with deposits of sand up to 100 m deep, borne from the surrounding desert by the prevailing northeasterly winds (Chaves, 1953; Macdonald, 1964).

CLIMATE

The peninsula lies entirely within the anomalous South Caribbean Dry Zone, which extends from Trinidad westward as far as Cartagena, Colombia (Map 4). The zone includes all parts of the coastal region where annual rainfall is less than 1000 mm (Lahey, 1958; Snow, 1976). The aridity of Guajira is caused by the combination of persistent northeasterly winds and a relatively cool sea surrounding the peninsula (Chaves, 1953). The coolness of the sea is due to upwelling of cold water from the depths to the north and east (Snow, 1976). The atmospheric humidity is too low for cloud formation, except where the airstream is forced up by the steep slopes of the Serranía de Macuira. Since the wind velocity is high and the clouds are rapidly formed on the windward side of the hills and equally rapidly dissipated on the lee-
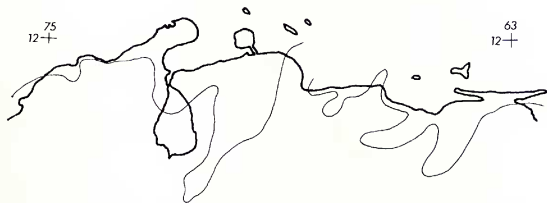
Map 4. Southern limit of South Caribbean Dry Zone (adapted from Lahey (1958) and Snow (1976)).

ward side, rainfall is a rare event. From mid-September to mid-November, however, the Trade-Wind Belt is at its maximum northern displacement and the peninsula is embraced by the Equatorial Zone of atmospheric convergence. During this season the winds are mostly southwesterly, humid, and moderate; there is extensive cloud formation and considerable precipitation over the entire peninsula (FIGURE 1), transforming large tracts of land into impassable quagmires. The mean annual precipitation in the lowlands is 355 mm and is quite variable; a total of 100 mm fell in 1941, followed by 680 mm in 1942 (Chaves, 1953). The mean monthly temperature is 28° C and varies little throughout the year. Absolute minima and maxima recorded by Chaves (1953) were 14 and 40° C, respectively.

There are virtually no climatic records from the upper slopes of the Serranía de Macuira. The few data presented by Sugden and Robins (1979) suggest a temperature lapse rate of ca. 1° C per 100 m, with a mean tem-
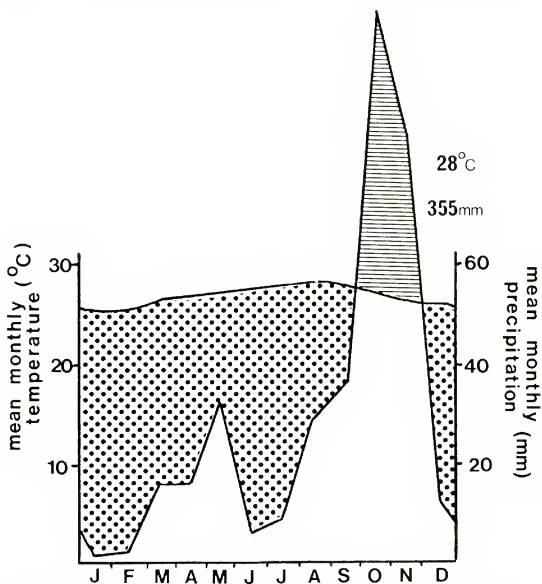

FIGURE 1. Climatic diagram for Guajira, drawn from the data of Chaves (1953).

perature of ca. 22.5° C at 500 m. The important point is that, according to my experience and that of reliable local informants, rainfall occurs on the upper slopes only when also occuring in the surrounding lowlands, although it is not known whether the quantity differs. Otherwise, the only precipitation is through cloud interception by the vegetation.

Small, fair-weather cumulus and lenticular clouds are present over the Serranía de Macuira during the day, but they rarely envelop the peaks. During early evening, however, nimbostratus develops on the windward side of the hills, often some kilometers toward the coast, and by sunset on most days the slopes above 600 m are cloaked in a thick layer of low cloud. The cloud base is always lower on the windward side of the hills, and at dawn it is often down to 350 m. TABLE 1 shows the results of observations made during March, April, and May, 1977, of the cloud cover on two prominent (565 and 710 m high) peaks. If it is assumed that the clouds do not disperse during the night and reform by dawn (an assumption that is supported by the experience of a month of soaking nights in a camp at 600 m), it can be concluded that the clouds remain for at least 12.5 hours at 550 m on 77 percent of the nights observed, and for at least 12.5 hours at 700 m on 95 percent of nights. The gaps in the records in TABLE 1 are due to nights when the clouds descended after dark; on most such occasions, however, clouds were present on the slopes at dawn the following day—only twice were they entirely absent. The highest peaks, Palua and Huarech, were occasionally observed to remain in cloud for up to 36 hours.

VEGETATION

The dry vegetation types of Guajira have been described by Espinal and Montenegro (1963) and by Rieger (1976). Espinal and Montenegro, using the Holdridge Life Zone system of classification, divided the vegetation of the peninsula into two main zones: an inland zone of Tropical Thorn Woodland (Monte Espinoso Tropical), extending from the base of the peninsula and encompassing the three serranías; and a coastal zone of drier Desert Scrub (Maleza Desertica). In their ecological map of the region, they depicted a small zone of Very Dry Tropical Forest (Bosque Muy Seco Tropical) on the slopes of the Serranía de Macuira and the northeastern flanks of the Serranía de Jarara, and a zone of Subtropical Humid Forest (Bosque Húmedo Subtropical) on the summits of the Serranía de Macuira (TABLE 2).

Rieger (1976), in a more detailed analysis using Braun-Blanquet phytosociological techniques, divided the dry vegetation of the peninsula into twenty associations falling into six major groups. In a transect across Jiborne, the southernmost high peak of the Serranía de Macuira, he recognized seven associations (TABLE 2).

My view of the vegetation is somewhat different in its details from the descriptions of these authors, partly because I had the opportunity to spend more time exploring the Serranía. Qualitative observations made during July, August, and September of 1975 and March, April, May, July, and August

TABLE 1. **Period of cloud cover* on consecutive nights at different altitudes on the Serranía de Macuira.**

DATE	ALTITUDE		DIFFERENCE
	550 m	700 m	
March 22/23	14.5	18.0	3.5
	12.5	14.0	1.5
	13.0	14.5	1.5
	13.0	16.0	3.0
	17.0	19.0	2.0
	13.0	15.5	2.5
	—	14.0	—
	12.5	15.0	2.5
	14.0	15.5	1.5
	14.0	15.5	1.5
	15.5	17.0	1.5
	—	14.5	—
April 3/4	—	14.0	—
April 6/7	15.0	20.0	5.0
	14.5	17.0	2.5
	13.0	14.5	1.5
	13.0	14.5	1.5
	15.0	19.0	4.0
	15.0	16.5	1.5
	—	15.0	—
	15.0	19.0	4.0
	14.5	18.0	3.5
	14.0	17.0	3.0
	16.0	18.0	2.0
	16.0	17.5	1.5
	14.5	16.5	2.0
	—	14.5	—
	13.5	15.0	1.5
	13.0	14.5	1.5
	14.0	18.0	4.0
	—	14.0	—
	12.5	14.5	2.0
	—	15.5	—
	13.5	16.0	2.5
	13.0	15.0	2.0
	13.0	15.0	2.0
	—	13.5	—
	—	—	—
	—	—	—
	13.0	15.0	2.0
	14.0	15.5	1.5
	15.5	17.0	1.5
	15.5	18.5	3.0
May 6/7	13.5	14.0	0.5

*Measured in hours.

TABLE 2. **Vegetation types of the Serranía de Macuira:**
comparison of different classifications.

ESPINAL & MONTENEGRO (1963)	SUGDEN (present paper)	RIEGER (1976)*
Monte Espinoso Tropical	Thorn Woodland	*Bursera glabra* woodland
Bosque Muy Seco Tropical	Very Dry Deciduous Woodland	*Lonchocarpus punctatus* forest *Astronium graveolens–Tabebuia bilbergii* woodland *Bursera graveolens* woodland
	Dry Evergreen Forest	Evergreen thicket dominated by Capparaceae *Eugenia umbellulifera* woodland
(No equivalent)	Riparian Vegetation	*Vitex cymosa–Libidibia coriaria* woodland
Bosque Húmedo Subtropical	Cloud Forest	*Rapanea guianensis* woodland (Elfin Woodland)

*This comparison is not intended to contest the validity of Rieger's associations; these are recognizable subdivisions of the major vegetation types described in this paper.

of 1977 indicate that there are four principal vegetation types on the lower slopes of the Serranía, which may be distinguished by their physiognomy, their leaf morphology and phenology, and the presence or absence of certain indicator species. These are Thorn Woodland, Very Dry Deciduous Woodland, Riparian Vegetation, and Dry Evergreen Forest (TABLE 2), occurring respectively on well-drained sand deposits, on steep, micaceous schist slopes on outlying hills, on the banks and beds of arroyos (seasonal streams and rivers), and on the sheltered slopes of the larger (to 500 or 600 m) hills. Rieger's (1976) associations are subdivisions of some of these categories (TABLE 2). The characterization of vegetation types is particularly difficult because of the extent of human activity in the region and the abundance of secondary vegetation types.

THORN WOODLAND

Most of Guajira is covered with this type of vegetation. In the Serranía de Macuira it occurs on the deep deposits of sand that cover the northeastern slopes and is characterized by evergreen, leptophyllous (*sensu* Raunkiaer, 1934), flat-topped, leguminous trees 5–10 m tall (e.g., *Prosopis juliflora* (Sw.) DC. and *Libidibia coriaria* (Jacq.) Schlechter) and by deciduous trees such as *Bursera glabra* Triana & Planchon. The canopy varies from quite

open to dense and is frequently interrupted and overtopped by large cacti, especially *Lemaireocereus griseus* (Haw.) Britton & Rose. The undergrowth is variable and is generally thicker where the canopy is broken. *Croton rhamnifolius* H.B.K. and *Cordia curassavica* (Jacq.) Roemer & Schultes are the most frequent species, the former favoring the more shaded habitats and often forming pure stands. Scattered individuals of the evergreen shrubs *Bunchosia odorata* (Jacq.) H.B.K., *Calotropis procera* R. Br., *Hippocratea verrucosa* H.B.K., and *Melochia tomentosa* L. occur throughout the formation. There is virtually no ground cover apart from small individuals of *Opuntia* spp. With the exception of rare colonies of *Tillandsia flexuosa* Sw., epiphytes are absent. Woody lianas such as *Arrabidaea mollissima* (H.B.K.) Bur. & K. Schum. and *Banisteriopsis jasminellum* A. Juss. are, on the other hand, quite frequent.

There is no doubt that this vegetation is highly disturbed by human activity. The Guajiro favor the extensive ridges and hummocks of sand between the watercourses as dwelling places for several reasons: the sand has the right combination of softness and firmness for the foundations of wood-pile huts, and there is relative ease of access to water, safety from the annual floods, and freedom from mosquitoes. Because water is less scarce than it is elsewhere in Guajira, the human population is quite dense, and the Thorn Woodland has therefore suffered the depredation of domestic animals, particularly goats. Additionally, trees are frequently felled for the construction of corrals and enclosures. There appears to be little regeneration of canopy species; the prevalence of *Cordia curassavica* and *Croton rhamnifolius* in the undergrowth may be due to their unpalatability to goats.

Very Dry Deciduous Woodland

The boundary between Thorn Woodland and Very Dry Deciduous Woodland (Figure 2) is usually marked by an abrupt change in topography and substrate. Wherever the steep, micaceous schist slopes of the Serranía emerge from the blanket of sand, whether at 50 or 200 m, the leptophyllous, evergreen, leguminous trees are replaced by taller, microphyllous or mesophyllous species. The canopy is variable in height, reaching a maximum of ca. 20 m in sheltered sites and decreasing to as little as 5 m on windward slopes. Some more common species of canopy trees in this vegetation are *Astronium graveolens* Jacq., *Bursera simaruba* (L.) Sarg., *Cochlospermum vitifolium* (Willd.) Sprengel, *Lonchocarpus punctatus* H.B.K., and *Sapindus saponaria* L. Most canopy species produce a flush of leaves at the beginning of the rainy season or a few weeks before and shed them between January and March, remaining leafless for six to eight months of the year.

There is a very broken understory of evergreen Capparaceae, including several species of *Capparis*. The leaves of *C. coccolobifolia* Martius ex Eichler and *C. pachaca* H.B.K. are coriaceous and glabrous, while those of *C. tenuisiliqua* Jacq. are chartaceous and pubescent; those of *C. linearis* Jacq. are narrowly linear and coriaceous. The ground layer is very sparse, consisting of scattered individuals of *Opuntia* sp., *Elytraria imbricata* (Vahl) Pers., *Isocarpha oppositifolia* (L.) R. Br., and *Ruellia inundata* H.B.K.; the

FIGURE 2. Very Dry Deciduous Woodland, ca. 200 m alt.

stems of a scandent *Philodendron* are frequently found trailing across the substrate toward the upper limit (ca. 400 m) of the Very Dry Deciduous Woodland. Climbers and epiphytes are rare; colonies of epiphytic *Tillandsia flexuosa, Brassavola nodosa* Lindley, and *Schomburgkia humboldtii* Reichenb. f. were each seen on two occasions.

The soil is hard and shallow, and much of the surface consists of bare rock and compacted or loose stone fragments. Organic matter generally accumulates in crevices and gullies. Most of the dry litter is washed away during the annual rains due to the steeply sloping terrain.

It appears that little regeneration of canopy species is occurring, once again due to the ravages of goats, which are allowed to wander some distance from the farmsteads. *Jatropha urens* L., a stinging, unpalatable shrub, is avoided by goats and is consequently common in the Very Dry Deciduous Woodland.

The upper and lower limits of this formation are variable. On the smaller (300–600 m) outlying hills it extends to the summits. (On the neighboring Serranía de Jarara it covers the hills entirely.) On the higher, more extensive central hills around the principal peaks, the transition to Dry Evergreen Forest (see below) may occur as low as 250 m, especially in sheltered situations. The lower limit is contiguous with the upper limit of the sand deposits.

RIPARIAN VEGETATION

The numerous wide arroyos flowing through the foothills of the Serranía de Macuira are fringed by vegetation distinctly greener and more luxuriant than the dry types described above. Although these rivers are dry for most of the year, groundwater is always close to the surface and emerges at in-

tervals (usually where the basement rock outcrops and the layer of sand is thin or absent) as small streams. The streams disappear wherever the bed consists of deep sand or boulders.

While the Riparian Vegetation (FIGURE 3) is of limited extent compared to the other vegetation types, it warrants separate consideration because of the considerable number of species it contains that are absent elsewhere. Prominent among the woody species are *Anacardium excelsum* (Bert. & Balbis) Skeels, *Crateva tapia* L., *Vitex cymosa* Bert., and *Sapium aucuparium* Jacq., the first reaching a diameter of more than 1 m and a height of 25 m. Trees characteristic of Thorn Woodland and Very Dry Deciduous Woodland are quite frequent; *Prosopis juliflora*, *Astronium* spp., and *Lonchocarpus* spp. all grow to a greater size here than they do on the dry slopes and tend to retain their leaves longer. *Anacardium excelsum* and *Sapium aucuparium* are evergreen, with fairly coriaceous leaves, while *Crateva tapia* and *Vitex cymosa* have more or less membranaceous leaves that flush in February and March, when the dry season is already well advanced.

In the shade of these trees grows an understory of evergreen shrubs, especially *Annona glabra* L., *Hamelia patens* Jacq., and *Tabernaemontana amygdalifolia* Jacq.—species that are exclusive to this habitat. Lianas are more abundant here than in any other vegetation type in the Serranía; *Arrabidaea mollissima*, *Cardiospermum corindum* L., *Funastrum clausum* (Jacq.) Schlechter, *Momordica charantia* L., *Passiflora pulchella* H.B.K., and *Plumbago scandens* L. are all common. Epiphytes are very rare, as they are in the other low-altitude vegetation types.

Riparian Vegetation extends only a very short distance back from the banks

FIGURE 3. Riparian Vegetation, ca. 100 m alt.

of the arroyos—usually no more than 20 m and often much less if the banks are steep. Apart from the woody flora on the banks, there is also a characteristic flora of herbaceous annuals or ephemerals that grow in the riverbeds themselves during the dry season; these are evidently both moisture loving and heliophilic since they are mostly absent from the densely shaded banks. Grasses (e.g., *Chloris inflata* Link), sedges (*Eleocharis geniculata* (L.) Roemer & Schultes, *Mariscus rufus* H.B.K.), and composites (*Egletes prostrata* (Sw.) Kuntze, *Pluchea symphytifolia* (Miller) Gillis) are particularly abundant. Several ferns (*Adiantum concinnum* Willd., *Thelypteris* spp.) are commonly found on the shaded edges of permanent rock pools higher (300–500 m) in the mountains.

The obvious potential for cultivation in this habitat has been realized by the local people, who grow mangoes, coconuts, maize, papayas, tobacco, and other crops on the banks and in the beds of the arroyos. Livestock, especially cattle and swine, are watered and grazed. As a result, there is a great deal of disturbance, and it is certain that none of the Riparian Vegetation is primary except in the more inaccessible gullies.

DRY EVERGREEN FOREST

This vegetation (FIGURE 4) occurs on the larger central hills from ca. 250 to 550 m (600–650 m on the leeward side of the Serranía). The dominant trees are evergreen; the leaves (microphylls and mesophylls) are chartaceous to coriaceous and mostly simple. Common canopy trees are *Morisonia americana* L., *Clusia* sp., *Eugenia umbellulifera* (H.B.K.) Krug & Urban, *Ficus prinoides* (Humb. & Bonpl.) Willd., *Coccoloba* sp., and *Jacquinia revoluta*

FIGURE 4. Dry Evergreen Forest, ca. 350 m alt. Large bole left of center has d.b.h. of ca. 40 cm.

H.B.K., which attain heights of 8–15 m. The canopy is generally quite closed and shading. There is a well-developed understory containing small trees and shrubs 2–4 m tall; frequent species are *Acalypha diversifolia* Jacq., *Amyris sylvatica* Jacq., *Actinostemon concolor* (Sprengel) Mueller-Arg., *Aphelandra pulcherrima* (Jacq.) H.B.K., *Capparis baducca* L., *C. verrucosa* Jacq., *Hippocratea verrucosa*, *Psychotria microdon* (DC.) Urban, *Rauvolfia ligustrina* Roemer & Schultes, and *Ruellia macrophylla* Vahl. The ground layer is quite sparse, consisting mainly of *Petiveria alliacea* L. and occasional individuals of *Bromelia chrysantha* L. and *Elytraria imbricata*; seedlings and saplings of trees are quite common, indicating that there is less disturbance from man and livestock. Epiphytes are as rare as they are in the other dry formations, and lianas are infrequent.

The soil supporting the Dry Evergreen Forest is undoubtedly richer and better developed than that supporting the Very Dry Deciduous Woodland. There is a layer of dry litter several centimeters deep and a thin humus layer overlying a gray, crumbly mineral soil that varies in depth according to the proximity to the surface of the parent rock.

THE CLOUD FOREST

At 500–550 m on the windward side of the hills and 600–650 m on the leeward side, the dry formations give way to the Cloud Forest (FIGURE 5), which differs in nearly every respect from the surrounding vegetation. It has a different complement of species (including bryophytes and an abundance of vascular epiphytes), a smaller leaf size, a notable absence of compound leaves, and an often luxuriant undergrowth. The transition from dry seasonal vegetation to Cloud Forest is very abrupt, and the sudden increase in verdure and dampness is striking. The substrate is damp, and moisture drips from the vegetation, particularly in the morning after the clouds have lifted.

This vegetation is present on each of the three main peaks of the Serranía de Macuira, giving a total area of ca. 15 km² (MAP 3). Of all the vegetation types in the Serranía, it is the least disturbed by human activity. In 1977 the total area cleared for the grazing of cattle constituted only a small fraction of the Cloud Forest, and an estimated 95 percent of the vegetation was primary.

The vascular flora of the Cloud Forest is listed in TABLE 3 and is categorized into canopy trees, understory woody shrubs and coarse herbs, ground-cover herbs, epiphytes, ground-rooted climbers and scramblers, and hemiparasites. A total of 126 species were encountered, 14 of which are as yet incompletely identified; several species were encountered only once. TABLE 3 includes only those species collected during the course of the present study since the notes accompanying the small number of specimens collected by previous workers in the Cloud Forest do not accurately define the habitat of provenance. Species recorded by other collectors would increase the number of species in the table by a maximum of six. A few individuals of species common in the surrounding Dry Evergreen Forest (e.g., *Capparis baducca* and *Hippocratea verrucosa*) were encountered in the Cloud Forest but are not included in the table. Only four species (*Acalypha diversifolia*, *Actinos-*

FIGURE 5. Cloud Forest, 650 m alt., showing abundance of vascular epiphytes.

TABLE 3. **Ferns and flowering plants of the Cloud Forest.**

I. WOODY PLANTS OF THE CANOPY*

Pteridophyta	Blechnaceae	*Blechnum arborescens* (Klotzsch & Karsten) Hieron.
	Cyatheaceae	*Cyathea arborea* (L.) J. E. Smith
Dicotyledones	Apocynaceae	*Stemmadenia minima* A. Gentry
	Araliaceae	*Dendropanax arboreus* (L.) Dcne. & Planchon
	Boraginaceae	*Cordia macuirensis* Dugand
	Clusiaceae	*Clusia rosea* Jacq.
	Compositae	indet.
	Euphorbiaceae	*Euphorbia cotinifolia* L.
		Margaritaria nobilis L. f.
	Lauraceae	*Persea caerulea* (Ruiz & Pavon) Mez
	Melastomataceae	*Conostegia icosandra* (Sw.) Urban
		Miconia acinodendron (L.) Sweet
		Miconia laevigata (L.) DC.
		Mouriri rhizophoraefolia (DC.) Triana
	Moraceae	*Cecropia* sp.
		Ficus perforata L.
	Myrsinaceae	*Rapanea guianensis* Aublet
	Myrtaceae	*Myrcia fallax* (Rich.) DC.
		Myrcia splendens (Sw.) DC.
		Myrcianthes fragrans (Sw.) McVaugh
	Nyctaginaceae	*Guapira fragrans* (Dum.-Cours.) Little
	Ochnaceae	*Ouratea nitida* (Sw.) Engler
	Polygonaceae	*Coccoloba coronata* Jacq.
	Rubiaceae	*Genipa spruceana* Steyerm.
		Randia formosa (Jacq.) Schum.
		Rudgea marginata Standley

II. UNDERSTORY SHRUBS AND COARSE HERBS

Pteridophyta	Equisetaceae	*Equisetum giganteum* L.
Cycadales	Zamiaceae	*Zamia muricata* Willd.
Monocotyledones	Araceae	*Dieffenbachia* sp.
	Gramineae	*Gynerium sagittatum* (Aublet) Beauv.
		Olyra latifolia L.
	Marantaceae	*Maranta divaricata* Roscoe
		Stromanthe lutea (Jacq.) Eichler
	Musaceae	*Heliconia bihai* L.
		Heliconia latispatha Bentham
	Zingiberaceae	*Costus guanaiensis* Rusby
		Costus villosissimus Jacq.
		Renealmia occidentalis (Sw.) Sweet
Dicotyledones	Acanthaceae	*Aphelandra pulcherrima* (Jacq.) H.B.K.
		Ruellia macrophylla Vahl
	Amaranthaceae	*Alternanthera pubiflora* (Bentham) Kuntze
		Chamissoa altissima H.B.K.

TABLE 3 (*continued*).

	Compositae	*Baccharis trinervis* Pers.
	Euphorbiaceae	*Acalypha diversifolia* Jacq.
		Actinostemon concolor Mueller-Arg.
		Croton margaritensis J. R. Johnston
	Malvaceae	*Malvaviscus arboreus* Cav.
	Melastomataceae	*Clidemia hirta* (L.) D. Don
	Piperaceae	*Piper* sp.
	Portulacaceae	*Talinum paniculatum* (Jacq.) Gaertner
	Rubiaceae	*Chiococca alba* (L.) Hitchc.
		Guettarda divaricata (Humb. & Bonpl.) Standley
		Psychotria alba Ruiz & Pavon
		Psychotria barbiflora A. DC.
		Psychotria nervosa Sw.
		Spermacoce suffrutescens Jacq.
	Solanaceae	*Cestrum alternifolium* (Jacq.) O. E. Schulz
		Solanum hirtum Jacq.

III. GROUND LAYER

Pteridophyta	Adiantaceae	*Adiantum latifolium* Lam.
		Adiantum petiolatum Desv.
	Aspleniaceae	*Asplenium cristatum* Lam.
		Asplenium myriophyllum (Sw.) Presl
	Blechnaceae	*Blechnum occidentale* L.
	Aspidiaceae	*Polybotrya cervina* (L.) Kaulf.
		Tectaria incisa Cav.
	Lycopodiaceae	*Lycopodium cernuum* L.
Monocotyledones	Amaryllidaceae	*Zephyranthes tubispatha* Herb.
	Araceae	*Anthurium crassinervium* (Jacq.) Schott
	Cyperaceae	*Rhynchospora comata* (Link) Schultes
		Scleria secans (L.) Urban
	Gramineae	*Acroceras zizanioides* (H.B.K.) Dandy
		Coix lacryma-jobi L.
		Ichnanthus pallens (Sw.) Munro indet.
	Haemadoraceae	*Xiphidium caeruleum* Aublet
	Orchidaceae	*Campylocentrum micranthum* (Lindley) Rolfe
		Encyclia fragrans (Sw.) Lemée
Dicotyledones	Acanthaceae	*Ruellia malacosperma* Greenman indet.
	Compositae	*Erigeron bonariensis* L.
		Erechtites hieracifolia Raf.
		Liabum asclepiadeum Schultz Bip.
	Labiatae	*Scutellaria verecunda* Epling
	Leguminosae	*Desmodium axillare* (Sw.) DC.
	Passifloraceae	*Passiflora* sp.
	Solanaceae	*Solanum dulcameroides* Dunal
	Urticaceae	*Pilea microphylla* (L.) Liebm.

TABLE 3 (continued).

IV. EPIPHYTES

Pteridophyta	Grammitidaceae	*Grammitis blepharolepis* (C. Chr.) Morton
	Hymenophyllaceae	*Hymenophyllum hirsutum* (L.) Sw.
	Lomariopsidaceae	*Elaphoglossum* sp.
	Oleandraceae	*Nephrolepis rivularis* (Vahl) Mett.
	Polypodiaceae	*Microgramma lycopodioides* (L.) Copeland
		Microgramma piloselloides (L.) Copeland
		Polypodium maritimum Hieron.
		Polypodium phyllitidis L.
Monocotyledones	Araceae	*Anthurium scandens* (Aublet) Engler
	Bromeliaceae	*Guzmania cylindrica* L. B. Smith
		Guzmania lingulata (L.) Mez
		Guzmania monostachya (L.) Rusby ex Mez
		Guzmania sanguinea (André) André ex Mez
		Guzmania sp.
		Tillandsia anceps Lodd.
		Tillandsia bulbosa Hooker
		Vriesea heterandra (André) L. B. Smith
		Vriesea splendens (Brongn.) Lemée
	Orchidaceae	*Dichaea* sp.
		Elleanthus arpophyllostachys Reichenb.
		Epidendrum agathosmicum Reichenb. f.
		Epidendrum stenopetalum Hooker
		Jacquiniella globosa (Jacq.) Schlechter
		Maxillaria sophronitis (Reichenb.) Garay
		Pleurothallis ruscifolia R. Br.
		Polystachya foliosa (Lindley) Reichenb. f.
		Stelis sp.
Dicotyledones	Lentibulariaceae	*Utricularia alpina* Jacq.
	Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.
	Rubiaceae	*Hillia costanensis* Steyerm.

V. GROUND-ROOTED CLIMBERS AND SCRAMBLERS

Monocotyledones	Araceae	*Monstera* sp.
		Philodendron erubescens C. Koch & Augustin
Dicotyledones	Amaranthaceae	*Iresine argentata* (Martius) D. Dietr.
	Apocynaceae	*Mandevilla bella* (Pittier) Woodson
	Asclepiadaceae	*Cynanchum atrovirens* (Rusby) Sugden†

TABLE 3 (continued).

	Bignoniaceae	Schlegelia fuscata A. Gentry
	Leguminosae	Machaerium humboldtianum Vogel
	Passifloraceae	Passiflora sp.

VI. HEMIPARASITES

| Dicotyledones | Loranthaceae | Phoradendron sp. |

*Each species is listed under the category (I–VI) in which it most commonly occurs; not all species are exclusive to one category. For instance, a number of the epiphytic species are sometimes found growing on the ground, and some of the understory shrubs occasionally reach the canopy.

†**Cynanchum atrovirens** (Rusby) Sugden, comb. nov.

BASIONYM: *Metastelma atrovirens* Rusby, Descr. 300 New Sp. S. Am. Pl. 95. 1920.

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temon concolor, Aphelandra pulcherrima, and *Ruellia macrophylla*) were frequent in both formations.

Guapira fragrans, Rapanea guianensis, and *Myrcianthes fragrans* are the most frequent species in the canopy flora, accounting respectively for 41, 28, and 10 percent of the woody stems with d.b.h. greater than 1.5 cm. Most other species account for less than 1 percent of the woody stems in any size class. The three dominant species are morphologically similar in several respects, especially leaf size, texture, shape, and arrangement. The leaves are simple, glabrous, and elliptic to oval with cuneate bases; they have indistinct venation with the exception of the prominent midrib; they are tough, thick, and leathery, with a shiny cuticle on the adaxial surface only; the adaxial surface is much darker than the abaxial, and the petioles and internodes are short. The leaves of the less common canopy species are similar in most respects, although many are not as coriaceous as those of the dominant species. The spectrum of leaf size and the diversity of leaf shape of the woody species (canopy and understory) of the Cloud Forest are illustrated in FIGURE 6.

Rapanea guianensis has monopodial growth, and in sheltered sites the boles are usually quite straight and vertical (maximum d.b.h., 17.5 cm). branching only in the canopy. *Guapira fragrans* (maximum d.b.h., 35 cm) and *Myrcianthes fragrans* (maximum d.b.h., 27 cm) grow sympodially and are characteristically twisted and gnarled, branching at all levels and forming wider crowns than *R. guianensis*. The largest tree encountered in the Cloud Forest was an individual of *Dendropanax arboreus* with a d.b.h. of 41.5 cm.

The most frequent understory shrub is *Actinostemon concolor,* which occasionally reaches the canopy. Young individuals of the dominant canopy species are very frequent, as are the rubiaceous shrubs *Psychotria alba, P. nervosa, Guettarda divaricata,* and *Spermacoce suffrutescens.* The leaves of plants in the shrub layer are more variable than those of the canopy trees, and the internodes are longer. There is a greater range of size (FIGURE 6), less difference in color between the upper and lower surfaces, and a greater
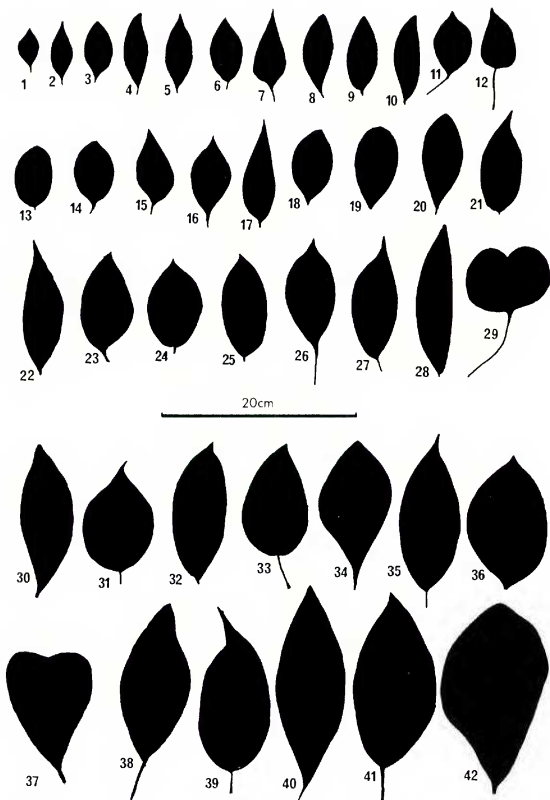
range in texture—from membranaceous (*Psychotria alba*) to coriaceous (*Actinostemon concolor*). As in the canopy, drip-tips and compound leaves are absent, and species with pubescent leaves (e.g., *Psychotria nervosa*) are few.

Other common components of the undergrowth are the cycad *Zamia muricata,* which has an underground stem and fronds up to 1 m long, and several large monocotyledons, particularly *Costus guanaiensis, Heliconia latispatha, Maranta divaricata,* and *Stromanthe lutea.* The occasional small swamps are populated by large heliophiles, especially *Dieffenbachia* sp., *Costus villosissimus,* and *Gynerium sagittatum.* Ground cover is provided by sparse grasses, sedges, ferns, bromeliads, a few herbaceous dicotyledons (e.g., *Scutellaria verecunda*), and the seedlings of trees and shrubs. The cover is by no means continuous, and there are large patches of bare soil and litter and frequent mossy boulders.

The epiphytes of the Cloud Forest have been discussed in detail by Sugden and Robins (1979) and by Sugden (in press). Although orchids are quite diverse (TABLE 3), bromeliads are the most conspicuous element of the vascular epiphytic flora, both in number of individuals and in biomass. Species of *Guzmania* grow on the boles and lower branches of the trees, while *Vriesea heterandra,* which is a smaller, more xeromorphic species, abounds in the canopy. On an individual of *Guapira fragrans* with a d.b.h. of 25 cm, 1035 bromeliads were counted, ranging in size from small juveniles 5 cm high to adult specimens of *Guzmania cylindrica* with leaves up to 1 m long (FIGURE 5). Mosses and hepatics are not prominent and do not festoon the branches as they do in similar vegetation in the Antilles (Beard, 1949). There is nevertheless a sparse growth of hepatics such as *Ceratolejeunea* spp., *Leptolejeunea* spp., and *Cololejeunea* spp. on the upper branches and in the canopy, and cushion-forming mosses are frequent on the boles close to the ground, especially on the highest peaks. Epiphylls are rare.

Ground-rooted climbers are few. *Philodendron erubescens* is frequent, as is a species of *Monstera;* occasional individuals of *Passiflora* sp. were observed. Only one species of parasite, *Phoradendron* sp., was encountered, at infrequent intervals.

FIGURE 6. Leaf size and shape in woody species of the Macuira Cloud Forest (silhouettes represent largest leaves on herbarium specimens of adult individuals): 1, *Myrcianthes fragrans;* 2, *Spermacoce suffrutescens;* 3, *Randia formosa;* 4, *Guettarda divaricata;* 5, *Chiococca alba;* 6, *Ficus perforata;* 7, *Iresine argentata;* 8, *Cordia macuirensis;* 9, *Cestrum alternifolium;* 10, *Stemmadenia minima;* 11, *Dendropanax arboreus;* 12, *Croton margaritensis;* 13, *Mouriri rhizophoraefolia;* 14, *Guapira fragrans;* 15, *Chamissoa altissima;* 16, *Mandevilla bella;* 17, *Alternanthera pubiflora;* 18, *Machaerium humboldtianum* (single leaflet of compound leaf); 19, *Rudgea marginata;* 20, *Rapanea guianensis;* 21, *Myrcia fallax;* 22, *Psychotria alba;* 23, *Psychotria barbiflora;* 24, *Coccoloba coronata;* 25, *Margaritaria nobilis;* 26, *Conostegia icosandra;* 27, *Miconia acinodendron;* 28, *Piper* sp.; 29, *Euphorbia cotinifolia;* 30, *Actinostemon concolor;* 31, *Clidemia hirta;* 32, *Ouratea nitida;* 33, *Solanum hirtum;* 34, *Psychotria nervosa;* 35, *Miconia laevigata;* 36, *Hillia costanensis;* 37, *Clusia rosea;* 38, *Ruellia macrophylla;* 39, *Acalypha diversifolia;* 40, *Aphelandra pulcherrima;* 41, *Persea caerulea;* 42, *Genipa spruceana.*

DIVERSITY OF HABITAT IN THE CLOUD FOREST. The overall impression given in the foregoing paragraphs is somewhat generalized. There is, in fact, considerable variation within the Cloud Forest, although not enough to warrant the division of the vegetation into anything more than minor subcategories, since the dominant trees are present throughout. Because of the dissection of the Serranía de Macuira into a labyrinth of small, steep valleys and ridges, levels of exposure to wind vary greatly according to aspect. The height of the canopy varies from 10 m in the most sheltered gullies to less than 1 m on the highest windswept peaks of Huarech and Palua. On the windward slopes boles and branches lean strongly uphill, often almost parallel to the ground (FIGURE 7), internodes are very short, and the low canopy has the appearance of a matted mass of tight rosettes. It is impossible to see the ground, and progress through this thicket is made only by clambering over the trees. This form of canopy continues over to the immediate sheltered sides of the sharp ridges, although the ground is in fact sloping the other way (FIGURE 7). Thus there is space for the growth of an understory, which is sheltered and heavily shaded as a result of the thick canopy. Further down the leeward slopes the canopy is more open since there is less disturbance from wind, and the trees are taller. Maximum canopy height is attained in the gullies, which afford more luxuriant and thicker growth than the leeward slopes, presumably because of the noticeably higher soil moisture content and the accumulation of organic matter and leached nutrients.

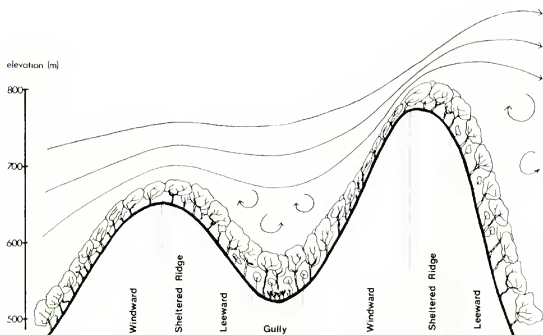The relative rarity of the majority of woody species in the Cloud Forest

FIGURE 7. Schematic representation of habitat diversity within the Macuira Cloud Forest.

creates difficulties in the quantification of any habitat preferences that might exist because a very large area would have to be surveyed to obtain a large enough sample. Additionally, the types of habitat outlined above (i.e., windward slope, sheltered ridge, leeward slope, and gully) are not always clearly demarcated; the variety of slope and aspect and the vagaries of topographical effects on the airstream ensure the existence of a range of intermediate habitats. In a quantitative survey in which all woody stems with d.b.h. greater than 1.5 cm were counted in 14 plots, each 98 m^2, the only clear result was that *Rapanea guianensis* was more abundant on windward than on leeward slopes.

Most of the larger herbaceous monocotyledons are more or less confined to the damp, shaded gullies; *Xiphidium caeruleum*, the two species of *Heliconia*, and *Stromanthe lutea* are good examples of species showing a strong preference for this habitat. The species of the few small swamps have already been mentioned.

The variation of habitat within the Cloud Forest is most strikingly shown by the vascular epiphytes. The most dense epiphytic populations occur on sheltered ridges (Sugden & Robins, 1979), and within this habitat there is an increase in both population density and species diversity with increasing altitude. Leeward slopes and gullies between 550 and 650 m support fewer species and smaller populations than do either sheltered ridges or windward slopes in the same altitudinal range. Windward slopes at higher altitudes are more impoverished than those at lower altitudes. These differences can be attributed to the variation with altitude of the daily period of cloud cover (TABLE 1), and to the variation with aspect of the cloud flux or throughput (Sugden & Robins, 1979; Sugden, in press a).

OUTLYING AREAS OF CLOUD FOREST. In addition to the three principal areas of Cloud Forest, there are at least two outlying peaks about 550 m high, each of which supports less than 1 ha of Cloud Forest on its summit. The two that were visited during the course of this study were Cerro Yauanauas and Cerro Ke'chuo (MAP 3). The former is separated from the Palua Cloud Forest, which is ca. 2 km away, by a steep-sided valley; the latter is separated from the Huarech Cloud Forest by a gentle saddle 0.5 km long, which dips to an elevation of ca. 450 m and is covered by Dry Evergreen Forest. The Cloud Forest species present on Cerro Yauanauas and Cerro Ke'chuo total 25 and 30, respectively; the two peaks have 16 species in common. Most of the commoner woody species of the Cloud Forest, including the dominant trees, are present on one or both of the peaks, while the herbaceous and epiphytic species are poorly represented.

The physiognomic and floristic transition from Dry Evergreen Forest to Cloud Forest is as abrupt on these hills as it is on the larger massifs. In both instances, the small patch of Cloud Forest is on the windward side of the peak, giving way to Dry Evergreen Forest on the leeward side within a few meters of the crest. It is probable that similar small patches of Cloud Forest are to be found on other outlying peaks over 500 m high (MAP 3), but these remain to be visited.

DISCUSSION

The important general features of the Macuira Cloud Forest are its isolation by surrounding arid lowlands and its clear dependence on cloud interception for its existence. Isolation from other moist regions poses interesting biogeographic questions concerning the origin and dispersal of the flora; these issues are discussed in separate papers (Sugden, in press b, 1982). Dependence on clouds is significant in the context of the classification of the Macuira Cloud Forest and may increase our understanding of the effects of cloud cover on tropical montane vegetation.

The Cloud Forest is similar in many respects to the Elfin Woodlands of Beard (1944, 1949, 1955) and Howard (1968, 1970, 1973), and to the Upper Montane Rain Forest of Richards (1952). The characteristics of Upper Montane Rain Forest, as tabulated by Grubb and Tanner (1976, *table 1*) and by Grubb (1977, *table 1*), include canopy height of 1.5–18 m, predominance of microphylls; usual absence of buttresses, cauliflorous trees, and drip-tips; paucity of compound leaves and climbers; and frequent occurrence of vascular epiphytes. The Macuira Cloud Forest has all of these features, although its abundance of vascular epiphytes is more characteristic of Lower Montane Rain Forest (see Grubb, 1977). The Elfin Woodlands of the summits of Antillean mountains (Howard, 1968) also fall into the broad category of Upper Montane Rain Forest, although the Macuira Cloud Forest differs from these at least in the relatively poor development of its bryophyte community. Both Howard (1968), in his extensive review of elfin vegetation, and Beard (1949) have stressed the abundance of bryophytes in Elfin Woodlands, where mosses and liverworts festoon the branches and often cover the forest floor. The Macuira Cloud Forest also lacks the aerial roots that were found to be common in an Elfin Forest on Pico del Oeste, Luquillo Mountains, Puerto Rico (Gill, 1969), and does not suffer the high level of leaf damage recorded in the same forest by Howard (1969); nevertheless, the two forests are similar in stature, leaf size and shape, and diversity of woody species.

Physiognomically, the Macuira Cloud Forest resembles the summit vegetation of Cerro Santa Ana (850 m), Edo. Falcón, Venezuela, and Cerro San Juan (930 m), Isla Margarita, Venezuela, more closely than any others (see above). The qualitative descriptions of these two mountains (by Tamayo (1941) and Johnston (1909), respectively) closely parallel that of the Serranía de Macuira. Both authors noted the importance of cloud interception on these mountains. The daily pattern of cloud cover and the contribution of direct rainfall to the precipitation on Cerro San Juan (Johnston, 1909) are apparently much the same as on the Serranía de Macuira.

In terms of the rapid transition from dry to moist vegetation, the Serranía de Macuira also resembles the Sierra de San Luis (1500 m), Edo. Falcón, Venezuela, which stands to the south of the Península de Paraguaná. The cloud forest on the Sierra de San Luis, however, begins at 1200 m (Steyermark, 1975) and has more diverse habitats and taller trees than does the Macuira Cloud Forest. Also, direct rainfall is of greater consequence; annual precipitation of up to 3000 mm has been recorded (Steyermark, 1975).

The Macuira Cloud Forest cannot be placed in any of the Life Zones of Holdridge (1967) and Holdridge et al. (1971). Mean temperatures of about 22° C and annual precipitation between 1000 and 5000 mm (which can be considered as reasonable lower and upper limits of precipitation in the driest and wettest parts of the Macuira Cloud Forest) are, according to the Holdridge model, the climatic conditions that support "subtropical" or "premontane" moist and wet forests. These forests bear no physiognomic resemblance to the Macuira Cloud Forest; rather, they are characterized by a canopy at least 20 m high, trees with spreading crowns, a well-developed understory layer, and few epiphytes. For this reason, Espinal and Montenegro's (1963) classification of the Macuira Cloud Forest as "Bosque Húmedo Subtropical" must be considered as erroneous.

Myers (1969) has also found the Life Zone model inadequate for the classification of Panamanian cloud forests. This may well be due to the fact that the model does not take into account the effect of clouds. Holdridge and colleagues (1971) admitted that cloud interception may significantly augment the total precipitation in a forest and noted that its quantity is dependent on the physiognomy and foliage characteristics of the vegetation. Nevertheless, undoubtedly because of the difficulty of quantifying cloud moisture interception, "it does not enter into the computation of mean annual precipitation of the Life Zone itself" (Holdridge et al., 1971, p. 47) but may be important in distinguishing vegetation associations within a Life Zone. In the case of the Serranía de Macuira, it is clear that cloud interception is of far greater importance than this.

The measurement of cloud interception by vegetation is troublesome. Kerfoot (1968) and Rutter (1975) have reviewed and summarized the many efforts to assess the levels of mist and cloud precipitation in various habitats, mostly in temperate regions. Shuttleworth (1977) has produced some theoretical considerations of the question. The essential problem is that since the magnitude of interception and subsequent precipitation is dependent on the stature and form of the vegetation, physical measurement using standard fog recording apparatus, such as gauze screens set above rain gauges, can give an idea only of the potential precipitation. Kerfoot (1968) concluded that the absolute values for cloud and mist interception were as yet conjectural, and it would appear that this state of affairs still prevails, especially in the neotropics.

Grubb and Whitmore (1966), in an extensive consideration of the importance of cloud cover in a montane forest in Ecuador, noted that droplet interception is likely to make a considerable contribution to overall precipitation but admitted the virtual impossibility of quantifying it. Baynton (1968, 1969) made a relative measurement of the amount of water extracted from impinging cloud on the summit of Pico del Oeste, Puerto Rico, but concluded that the interpretation to be placed on the measurement was not self evident; nevertheless, he estimated that cloud interception augmented the annual precipitation of 4530 mm by about 10 percent. In both localities difficulty in recording cloud interception was a consequence of the problem of distinguishing it from true rainfall. This problem is recognized by Rutter (1975)

as being one of the principal barriers to effective measurement.

Other effects of clouds, apart from precipitation, have also proved difficult to assess. Cloud cover is accompanied by high humidity and, during the daytime, low incident radiation; the water vapor pressure deficit, the light intensity, and the surface temperature are thereby reduced. These factors, and sometimes high winds, have been proposed by many authors to account directly or indirectly for many of the physiognomic features of wet montane forests.

High winds and low rates of transpiration, the latter resulting from the saturation of the air and the lowering of leaf temperature, have been suggested as major causes of stunted growth in cloud forests. Low rates of transpiration have been demonstrated in woody species of the Elfin Forests on the summits of Pico del Oeste (Gates, 1969) and Pico del Este (Weaver *et al.*, 1973), Luquillo Mountains, Puerto Rico. Weaver and colleagues suggested that this decreased the efficiency of base-pumping and ion uptake, thus lowering growth rates and causing stunting. Leigh (1975) also considered that the blocking of transpiration by the combination of atmospheric saturation and high winds (resulting in low rates of mineral uptake) is important in reducing the stature of montane forests subject to frequent cloud cover.

Grubb (1977) has disputed the importance of low transpiration rates, suggesting that the decrease in stature, biomass, and productivity in montane rain forests can be attributed primarily to lower temperatures and lower rates of photosynthesis, which are the expected results (Gates, 1969) of frequent cloud cover. Grubb pointed out that the primary factor limiting ion uptake is the availability of photosynthate for fueling active transport in the roots; the rate of transpiration does not affect the uptake of ions when they are at concentrations as low as those typical of most montane forest soils (Grubb, 1977). The slow rates of breakdown of organic material in the soil due to waterlogging, limited aeration, and the inherently slow rate of decay of coriaceous leaves (Grubb, 1971, 1977; Leigh, 1975) may also limit nutrient supply to the roots. Reduced rates of root respiration due to poor soil aeration may be an additional factor limiting uptake (Holdridge, 1967). Grubb (1977) also noted that the translocation of nutrients to young shoots, which takes place via the phloem, is not influenced by the rate of transpiration, although it can be expected to be affected by the availability of photosynthate. Leaching of minerals from the soil, particularly from ridges, may also contribute to stunting and slow growth rates (Baynton, 1969).

Tanner (1980b) suggested that the immediate cause of low stature in Upper Montane Rain Forest could be the reduced rate of wood production. In Mor Ridge forest in Jamaica (see Grubb & Tanner, 1976), he found that the annual biomass increment was very low, while the biomass of the standing crop of leaves was not very much lower than that in taller Lower Montane Rain Forests (Tanner, 1980a). He concluded that lower temperatures or water stress could not explain the stunting and impoverishment of Jamaican Upper Montane Rain Forests (Tanner, 1980b), favoring instead the low levels of nutrients and/or low levels of insolation as limiting factors (Tanner, 1980a).

The mechanical effects of high winds have been invoked as a further cause of the reduced stature of many cloud forests, particularly elfin forests on ridges and summits (Gleason & Cook, 1926; Leigh, 1975). While wind-pruning may be important on exposed ridges and slopes (Howard, 1970; Weaver *et al.*, 1973; Grubb & Tanner, 1976), gnarling and stunting also occur on sheltered slopes and gullies.

The tendency in Upper Montane Rain Forests toward coriaceous pachyphylls (see Grubb (1977) for definition of this term) with thick cuticles has been interpreted as a defense against the loss of minerals as a result of leaching from the leaves (Whitmore, 1975)—a likely consequence of frequent wetting by clouds and fog. It has also been suggested (Grubb, 1977) that the thickened palisade layer in tropical montane pachyphylls should result in high rates of photosynthesis per unit area, thus offsetting the effect of periods when cloud cover reduces light intensity and surface temperatures. The xeromorphy of these leaves may also enable them to withstand the fluctuations in humidity and incident radiation that occur as a result of the alternation of cloudy and cloud-free periods (Leigh, 1975). Pachyphylly does not, however, appear to confer any drought-resistant properties, since under controlled conditions these leaves dry out at rates similar to those of thinner, lowland rain forest leaves (Buckley *et al.*, 1980); this is in accord with Tanner's (1980b) contention that Upper Montane Rain Forests are not water stressed.

The relative abundance of epiphytes (both vascular and nonvascular) in cloud forests is due to regular bathing in clouds, which causes frequent precipitation and atmospheric saturation (Richards, 1952; Grubb & Whitmore, 1966; Johansson, 1974; Leigh, 1975; Grubb, 1977; Sugden & Robins, 1979). The epiphytic habit entails independence of the substrate for water and nutrients; the growth of epiphytes—especially those that are not xeromorphic or drought tolerant (Johansson, 1974)—is therefore favored by frequent precipitation and low saturation deficit. Cloud cover ensures the water supply during periods of negligible rainfall.

In the Serranía de Macuira it was possible to assess the distribution of epiphytic species in terms of cloud flux (Sugden & Robins, 1979; Sugden, in press a) simply because other factors—especially rainfall and the minimal variation in temperature due to the narrow altitudinal range of the Cloud Forest—did not complicate the interpretation of the results. While the Macuira Cloud Forest shares the characteristics of many stunted montane wet forests, it is not subject to low temperatures, high rainfall, and prolonged daytime cloud cover, and it therefore represents an excellent opportunity to resolve some of the outstanding questions concerning the effects of clouds on montane vegetation. On the basis of the present evidence, it would appear that the Upper Montane Rain Forest characteristics of the Macuira Cloud Forest do not result from low temperature (because of the low altitude), low insolation, or high winds. Water stress appears to affect the distribution of vascular epiphytes (Sugden, in press a), but not of woody species, in the Macuira Cloud Forest. Soils and mineral nutrition are therefore likely to be of key significance, and these aspects of the Macuira Cloud Forest now require investigation.

The new status of the Serranía de Macuira as a Colombian National Park will hopefully create favorable opportunities for future research oriented toward topics not covered in the present descriptive study. Conservation of the Cloud Forest is essential not only because of its intrinsic scientific interest but also to ensure continued irrigation, production, and prosperity in the valley and foothill settlements of the Serranía. The permanent groundwater in the arroyos is the direct result of cloud interception on the upper slopes, and one may confidently predict that extensive felling in the Cloud Forest would endanger this water supply. Felling for pasture may become a serious threat if regeneration in the surrounding dry vegetation continues to be prevented by overgrazing of goats.

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